

Alien spiders in Chile: evaluating Darwin's naturalization hypothesis

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Abstract. Darwin's naturalization hypothesis (DNH) states that the successful establishment of alien species is favored when the phylogenetic relationship between the colonizer and the recipient community is distant. From a population perspective, the establishment involves both the progressive increase in size and spatial distribution of the invasive population. In this study, we focused our attention on the spatial component of establishment, assessing the role of phylogenetic relatedness as a determinant of its extension. Following DNH, it is expected that alien species closely related to the native spiders would show narrower distribution ranges than alien taxa less related to the native species. We found 18 alien spider species in Chile; all of these are synanthropic and most are of African origin. Our results indicate a difference in range size between related and unrelated species but it was not statistically significant. Consequently, the results do not support DNH as an explanation of the distributional component of establishment of alien spider species in Chile. We conclude that ecological constraints do not affect the process of invasion of spiders; therefore, it is only time that determines the spread of alien spiders in this country.

Keywords: Aerial dispersal, biological invasion, geographic range, residence time, phylogenetic relatedness

Establishment of species beyond their natural range is on the rise because of increasing trade, transport, travel and tourism that are part of globalization. This provides living plants, animals and biological materials with vectors and pathways crossing the biogeographical barriers that would usually block their way (Shine et al. 2009).

Currently, organisms belonging to different taxonomic groups are translocated from one region to another, with which they do not share a prior history (Williamson 1996; Davis 2009). Although it is estimated that most of the organisms that disperse do not successfully establish in the target area, sometimes a small number of propagules can configure a founder colony and become established (Kolar & Lodge 2001; Sakai et al. 2001). One of the central challenges in the study of biological invasions has been to understand what factors determine this establishment process (Williamson 1996; Lockwood et al. 2007; Davis 2009), understood as a population expansion event.

Several hypotheses have been proposed to explain why some species are able to establish and others are not (Kolar & Lodge 2001; Mitchell et al. 2006). A particularly intriguing theory has been called Darwin's naturalization hypothesis (DNH) (Daehler 2001). This hypothesis, originally proposed by Darwin (1859), assumes that establishment success is influenced by the phylogenetic relationship between the colonizer and the members of the receiving community (Chesson 2000; Adler et al. 2007). In this context, invasive species that exhibit close phylogenetic relationships with the recipient community should display a high niche overlap, thus generating a high intensity of competition with members of the receiving community (Cahill et al. 2008; Cavender-Bares et al. 2009; Mayfield & Levine 2010). Therefore, under conditions of greater phylogenetic relationship to the recipient community, a colonizer would less likely establish oneself. Inversely, when the colonizer has a low level of relationship with members of the community, DNH suggests that competitive intensity decreases, a fact that will help to facilitate the establishment of

invasive species. Although there are various concepts of establishment (Richardson et al. 2000), from the population point of view, establishment can be visualized as a process in which a colony of alien species, once introduced, independent of intentional human assistance, has its population increase in size and expands into an area of colonization (Sakai et al. 2001; Shigesada & Kawasaki 2001). Thus, depending on the abundance and distribution levels, it is possible to recognize various stages of progress in the establishment process (Shigesada & Kawasaki 2001). Therefore, if the phylogenetic relationship determines the distribution component, as predicted by DNH, alien species more related to members of the community would show smaller distributional ranges when compared to those of less related taxa.

Generalist arthropod predators include invasive species that are capable of affecting native species through a variety of direct and indirect pathways (Snyder & Evans 2006). Invasive generalist arthropod predators can displace native predators primarily through competition, intraguild predation, transmission of disease, and escape from predation and/or parasites (Snyder et al. 2004). As generalist arthropod predators, spiders have the potential to affect native arthropod species assemblages; nevertheless, spiders have been largely overlooked as invasive species (but see Nyffeler et al. 1986; Hann 1990; Gruner 2005). Once established, invasive spiders may be viewed as either beneficial arthropods in agroecosystems, or as keystone predators in native ecosystems. Documented displacements of native spiders by invasive spider species are rare, although Nyffeler et al. (1986) and Hann (1990) reported cases of competitive exclusion between invasive and native spider species in Europe and New Zealand, respectively.

Because distributional range is one of the components of the establishment process, the objective of this study is to evaluate DNH and its effect on the distributional range of alien spiders in continental Chile. For this, we characterized the distributional ranges of alien spiders that differ in phylogenetic relatedness to native spiders, while also considering other

possible factors that can affect range size such as the minimum residence time (i.e., the time since the introduction of a species to a region) and aerial dispersal or ballooning (Thebaud & Simberloff 2001; Bell et al. 2005).

METHODS

Spider data and distributional range.—We used the World Spider Catalog (2014) for assigning the distribution of species in the world; also we complemented these data with an intensive literature survey and collections in different cities of Chile to determine the distribution in the national territory. We considered alien species that are not native to the country and/or have a cosmopolitan distribution in the world today, where the current distribution already reflects human influence. Single records of non-established spider species and doubtful records were excluded. From this information, the total number of administrative regions occupied by each species was established and then the latitudinal extension (in kilometers) was determined. For this purpose, the distributional range was estimated as the sum of the maximum length of each occupied administrative region (Instituto Geográfico Militar 2010); this procedure assumes that each species is distributed throughout each region (see Castro et al. 2005).

The phylogenetic relatedness between the alien spiders and resident community was classified in three levels. The first level (Close group) was used for species belonging to a genus that is represented in the native fauna of Chile. The second level (Intermediate group) was used for species belonging to genera not represented in the native spider fauna but from a family present in the native fauna. Finally, the third and most distant level (Distant group) was used for species belonging to genera and families not represented in the native spiders.

Because the area of origin is quite often not well known, the most probable origin of these spiders was taken from Kobelt & Nentwig (2008). The alien spider origins were attributed to the following five categories: a) Africa, b) Asia, c) Europe, d) America (refers to the tropical part of America) and e) “unknown” when the origin of some alien spider species is not exactly known but the species is globally distributed.

The minimum residence time was obtained from the oldest known record of the species obtained from historical information and collections. In addition, a measure of aerial dispersal, or ballooning, was included at an ordinal scale of 0 = not known, 1 = present, based on Bell et al. (2005).

Statistical analyses.—We performed a Generalized Linear Model (GLM) with normal error structure and the identity link function using STATISTICA 6.0 program (Stat Soft 1999) for analyzing simultaneously the effect of categorical (dispersal mode, phylogenetic relatedness) and continuous (residence time) variables on the dependent variable (distribution range, in km). The normality of residuals was analyzed with a Kolmogorov-Smirnov test after fitting the model. Phylogenetic relatedness was used to test DNH where dispersal mode and residence time were tested for other ecological factors that can explain distribution range.

RESULTS

Taxonomy of alien species and distribution in Chile.—We found 18 alien species belonging to 11 families. All alien spiders in this study are synanthropic species with 13 being

considered cosmopolitan (Table 1), where Theridiidae were represented by four species, the most abundant family. The families Araneidae, Agelenidae, Pholcidae, and Salticidae were represented by two species each. Six other families are represented by only one species. The most astonishing aspect of the composition of the alien spider fauna is that it does not reflect the structure of the Chilean spider fauna. Only eight of the 11 families of alien spiders are also present in Chile. The families Agelenidae, Oecobiidae and Dysderidae are not represented in the native fauna (Fig. 1). Many of the spiders are of African origin (33.3%), followed by European (27.7%) and Asian species (22.2%) and finally South American species (5.5%), however, the biogeographical origin of the other species is unknown. The species of European origin are those with the highest average distributional range in Chile (2081 km), followed by the species of Asian origin (1738 km) (Table 2).

The regions with the highest number of alien species are the Tarapaca region (11 species) and the Antofagasta region (10 species) in northern Chile (Fig. 2). The spiders *Pholcus phalangioides* (Fuesslin 1775) (Pholcidae) and *Steatoda grossa* (C. L. Koch 1838) (Theridiidae) are the most widely distributed in Chile, being found from Arica (18° 28' S, 70° 52' W) to Magallanes (53° 9' S, 70° 55' W). Other species widely distributed in Chile are *Dysdera crocata* C. L. Koch 1838 (Dysderidae), *Tegenaria domestica* (Clerck 1757) (Agelenidae), *Menemerus semilimbatus* (Hahn 1827) (Salticidae), *Urozelotes rusticus* (L. Koch 1872) (Gnaphosidae) and *Oecobius navus* Blackwall 1859 (Oecobiidae). The species *Hasarius adansoni* (Audouin 1826) (Salticidae), *Latrodectus geometricus* C. L. Koch 1841 (Theridiidae), *Heteropoda venatoria* (Linnaeus 1767) (Sparassidae) and *Smeringopus pallidus* (Blackwall 1858) (Pholcidae) are found exclusively in the north of Chile (Table 1).

Minimum residence time.—Only three species had a minimum residence time greater than 100 years. Most species have a residence time between 1 and 24 years (Table 2). GLM analysis showed a significant positive effect of the minimum residence time on the size of the distributional range (Fig. 3) (GLM, $F_{1, 11} = 37.7$, $P < 0.05$). Spiders with longer residence time in the country include *P. phalangioides*, *T. domestica*, *S. grossa*, *D. crocata* and *U. rusticus* (Table 1).

Darwin's naturalization hypothesis and distributional range.—Twenty eight per cent of alien species belong to a phylogenetically related group. Exactly half of the species belong to families already represented in the native fauna (Intermediate group); while the distant group represented only 22% of the alien species. The set of species with higher levels of phylogenetic relationship (Close group) with native fauna (i.e., congeneric species) had an averaged distribution range of 1452.2 km, while those distant species (Distant group) showed the greatest geographical extension (1710 km), but these differences were not statistically significant (GLM, $F_{2, 11} = 0.4$, $P = 0.65$). The aerial dispersal did not affect the distribution range (GLM, $F_{1, 11} = 0.9$, $P = 0.35$).

DISCUSSION

We can say that the effect of residence time can be interpreted as a neutral hypothesis; only time of arrival of alien spiders is enough to predict invasiveness. If this is true,

Table 1.—List of alien species, their earliest records, biogeographical distribution, and distribution in Chile. Area of origin: since the area of origin is quite often not well known, this refers to the most probable origin.

Taxa	Area of Origin	Geographic distribution	First record in Chile	Distribution in Chile
Araneidae				
<i>Argiope trifasciata</i>	Africa	Cosmopolitan	Levi (1968)	From Salamanca to Lanquihue
<i>Zygiella x-notata</i>	Unknown	Cosmopolitan	Mello-Leitão (1951)	Very common in southern Chile, Santiago to Los Lagos Region.
Agelenidae				
<i>Tegenaria domestica</i>	Europe	Cosmopolitan	Simon (1904)	Center of Chile to Magallanes region
<i>Tegenaria pagana</i>	Europe	Europe to Central Asia, USA to Chile, New Zealand	Roth (1968)	Center of Chile: Metropolitan and Valparaíso region
Dysderidae				
<i>Dysdera crocata</i>	Europe	Cosmopolitan	Nicolet (1849)	From Antofagasta to Bio-Bio Region
Oecobidae				
<i>Oecobius navis</i>	Africa	Cosmopolitan	Santos & Gonzaga (2003)	North and center of Chile: From Iquique to Bio-Bio Region
Pholcidae				
<i>Pholcus phalangioides</i>	Asia	Cosmopolitan	Nicolet (1849)	From Arica to Magallanes Region
<i>Smeringopus pallidus</i>	Africa	Pantropical	Taucare-Ríos (2012)	North of Chile: Tarapacá Region
Prodidomidae				
<i>Prodidomus rufus</i>	Unknown	Cosmopolitan	Platnick & Baehr (2006)	Antofagasta Region
Gnaphosidae				
<i>Urozelotes rusticus</i>	Asia	Cosmopolitan	Simon (1904)	Atacama to Valparaíso Region
Salticidae				
<i>Hasarius adansoni</i>	Africa	Cosmopolitan	Taucare-Ríos (2013b)	Arica and Parinacota and Tarapacá Region
<i>Meuemerus semilimbatus</i>	Africa	Canary Islands, southern Europe, western Asia, and Africa; and introduced to Argentina, Chile, and USA.	Taucare-Ríos & Edwards (2012)	Arica and Parinacota to Maule Region
Scytodidae				
<i>Scytodes univittata</i>	Asia	Canary Is. to Myanmar, synanthropic in Neotropics	Brescovit & Rheims (2000)	From Arica to Chañaral
Sparassidae				
<i>Heteropoda venatoria</i>	Asia	Pantropical	Taucare-Ríos & Brescovit (2011)	Tarapacá Region: Iquique
Theridiidae				
<i>Latrodectus geometricus</i>	Africa	Cosmopolitan	Taucare-Ríos (2011)	From Arica to Mejillones
<i>Parasteatoda tepidariorum</i>	South America	Cosmopolitan	Levi (1967)	North to center of Chile: Antofagasta to Santiago
<i>Steatoda grossa</i>	Europe	Cosmopolitan	Simon (1904)	From Arica to Magallanes
<i>Steatoda triangulosa</i>	Europe	Cosmopolitan	Taucare-Ríos et al. 2013	Tarapacá Region

then the effect of other ecological variables is not significant. We failed to prove that the aerial dispersal and the interspecific competition between phylogenetically related species (DNH) would play a significant role in the invasion success of the alien spiders in Chile. The distributional range increased in size as residence time in the invaded region increased.

The number of alien species represents about 2% of known spiders in Chile. The family Theridiidae includes the largest

number of alien species, agreeing with the results obtained by Kobelt & Nentwig (2008). Apparently the species of this family have a predisposition to be alien due to their link with human dwellings (Kobelt & Nentwig 2008). Globally common families, such as Tetragnathidae, Lycosidae and Zodariidae, are not represented at all among the alien species in Chile, probably because some families are usually not associated with human infrastructure and have a rather low probability of becoming transported to foreign areas (Kobelt & Nentwig

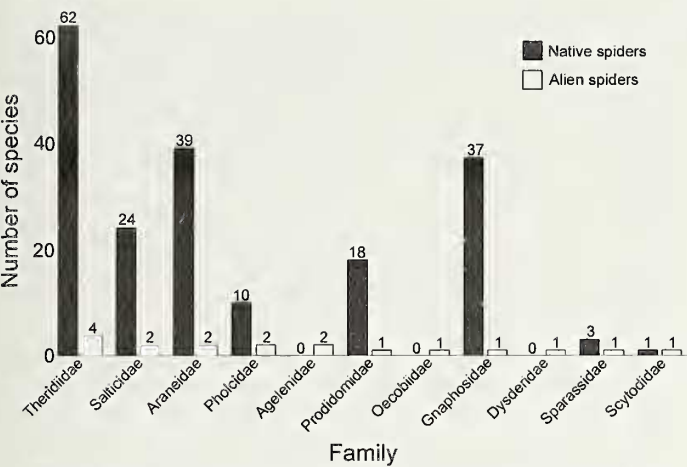


Figure 1.—Taxonomic overview of alien spider species in Chile compared to the native Chilean fauna. Families are presented in decreasing order based on the number of alien species.

2008). Most alien spiders are of African origin, which is consistent with the results obtained by Kobelt & Nentwig (2008), and currently have cosmopolitan distributions (*Argiope trifasciata* (Forsskal 1775), *H. adansoni*, *O. navus* and *L. geometricus*) (Levi 1968; World Spider Catalog 2014). However, the species with the highest distributional range were the spiders of European origin, namely: *D. crocata*, *S. grossa* and *T. domestica* (Simon 1904; Roth 1968; Levi 1967; Ramirez et al. 2004; Taucare-Rios et al. 2013) (Table 2). A comparison between temperate and tropical origins indicates

Table 2.—Size of the geographic range (mean \pm SD) for 18 species of alien spiders inhabiting continental Chile. This information is organized according to the minimum residence time, aerial dispersal, biogeographic origin and the phylogenetic relatedness.

Factors	Size [km]	N
Minimum residence time		
160 years	2868.5 \pm 1416.3	2
110 years	2574.6 \pm 1144.2	3
63 years	1309 \pm 0.0	1
47 years	1317.6 \pm 17.5	3
22 years	1441.0 \pm 0.0	1
14 years	1257.0 \pm 0.0	1
8 years	378.0 \pm 0.0	1
3 years	422.0 \pm 384.0	2
2 years	779.2 \pm 612.5	4
Biogeographic origin		
Asia	1738.2 \pm 1557.2	4
Europe	2081.0 \pm 631.9	5
Africa	963.1 \pm 631.9	6
Unknown	614.0 \pm 333.7	2
America	1318.0 \pm 0.0	1
Aerial dispersal		
Not known	1113.8 \pm 701.0	8
Present	1618.3 \pm 1331.8	10
Phylogenetic relatedness		
Close group	1452.2 \pm 1425.6	5
Intermediate group	1226.1 \pm 1176.9	9
Distant group	1710.0 \pm 397.8	4

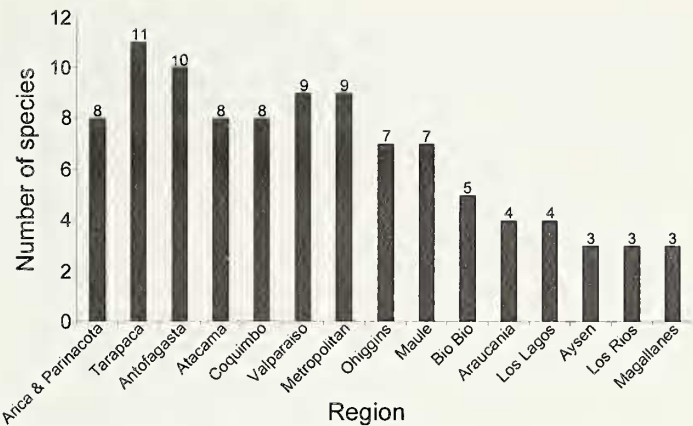


Figure 2.—Number of alien spider species for each region of Chile. Arranged from north to south.

that about 30% of the species originate from temperate habitats (Europe) and about 60% are from the tropical habitats (Asia, Africa and America); the climate habitats of the others are unknown. Uncertainty, however, is high because for many species very little is known about the natural environment in which they live in the area of origin.

Residence time is a critical variable to predict invasiveness (Wilson et al. 2007), a fact that is reinforced by our results. The species with the highest residence time in Chile were *P. phalangioides* and *D. crocata*, described and reported for the first time in Chile over 160 years ago by Nicolet (1849). Similarly *Urozelotes rusticus*, *Tegenaria domestica* and *Steatoda grossa*, reported by Simon (1904), had a minimum residence time of about 110 years. To date, these species have significantly expanded their distribution in the country invading from the arid climate of northern Chile through the humid and cold climates in south Chile (Simon 1904; Cekalovic 1976; Platnick & Murphy 1984; Taucare-Rios 2010; Taucare-Rios et al. 2013). Other species reported in Chile have a wide distribution. These species include *M. semilimbatus*, *Scytodes univitatta* Simon 1882, *Zygiella x-notata* (Clerck 1757) and *O. navus* (Mello-Leitão 1951; Levi 1974; Brescovit & Rheims 2000; Santos & Gonzaga 2003;

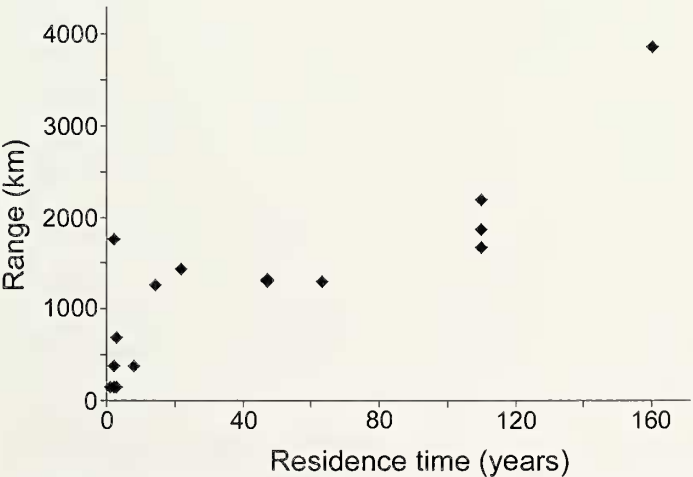


Figure 3.—Relationship between residence time and distributional range of alien spider species.

Taucare-Rios & Edwards 2012; Taucare-Rios 2013a; Taucare-Rios et al. 2013). Finally, species reported recently, such as *L. geometricus*, *S. pallidus*, *H. adansonii*, *Prodidomus rufus* Hentz 1847, and *H. venatoria*, have a limited distribution in Chile (Platnick & Baehr 2006; Taucare-Rios & Brescovit 2011; Taucare-Rios 2011, 2012, 2013b); these results show a clear correlation between the minimum residence time and distributional range of the species. Other studies have also suggested a positive relationship between residence time and current distribution of alien species (Rejmánek 2000; Castro et al. 2005; Hamilton et al. 2005; Wilson et al. 2007).

Shipping traffic is responsible for the majority of accidental generalist arthropod predator introductions (Snyder et al. 2004). For example, the ground beetle *Pterostichus melanarius* Illiger 1798, a European native that has invaded a large part of North America, is believed to have arrived in soil ballast dumped from ships (Niemela et al. 1997). Also it is known that potted plants and container shipments with manufactured goods are important modes of introduction for alien arachnids (Kobelt & Nentwig 2008; Nentwig & Kobelt 2010). In Chile, most of the alien species are present in coastal regions (e.g., Tarapaca, Antofagasta, and Valparaíso Regions), where they probably arrived because of commerce and the relocation and travel of people; and from there they were transported by humans to other localities. It is known that some alien spider species may have been introduced to the northern ports (Taucare-Rios 2011; Taucare-Rios & Brescovit 2011; Taucare-Rios & Edwards 2012), including pantropical and cosmopolitan species from Asia and Africa, such as *M. senilimbatus*, *H. venatoria*, *P. phalangioides*, *S. pallidus* and *L. geometricus*.

The modes of range expansion in spiders vary. For example, small web-building spiders naturally spread by means of ballooning. By this means, they can be transported hundreds of kilometers with the help of air currents (Bell et al. 2005). However, ballooning is not regularly used by large invasive species (Walter et al. 2005). Such species and non-ballooning species must have used other means, in particular human mediated transfer (cf. Rabitsch 2011). Thus, the contribution of aerial dispersal in the alien spiders in Chile is less important compared to the facilitated transport by humans.

Finally, we can say that our results do not support DNH as a plausible explanation of the distributional component of establishment of alien spiders in Chile. This hypothesis arose from a related hypothesis of Darwin (1859) that closely related species tend to possess similar niches and, hence, perform similarly under the same environmental conditions (for a recent empirical example, see Brandt et al. 2009), translating into strong competition imposed by resident species on closely related invaders that reduces their success. Within this context, there have been multiple attempts at testing DNH (reviewed in Proches et al. 2008). Together, these studies have reported positive (Daehler 2001; Duncan & Williams 2002), negative (Rejmanek & Richardson 1996; Strauss et al. 2006), or no (Lambdon & Hulme 2006; Ricciardi & Mottiar 2006) agreement with DNH. However, DNH best applies to small spatial scales at which species interact with each other. Given the assumption of strong competition between closely related species as a driving mechanism (Proches et al. 2008), it does not always happen, since competition may not be relevant to some alien species.

Our results show that all alien spider species in the country are synanthropic and may not compete strongly with native species which do not usually inhabit urban environments, therefore, maybe competition is not relevant in the establishment of the alien spiders in Chile. Others factors could be more important for these animals in anthropogenic environments. For example, it is known that on a geographic level, macro-environmental conditions (climate, precipitation, temperature, etc.) do influence the size of a species' range, even more than do interspecific interactions (see also Chesson 2000; Hubbell 2001; McKinney 2006; Sax et al. 2007).

This work summarizes knowledge about the alien spiders in Chile and the ecological process that may determine their establishment. In this context, our results do not support DNH, but do show the importance of minimum residence time for the establishment process of the alien spiders in Chile. Early warning plans will be very efficient to control the invasion of alien spiders, because in the absence of ecological constraints, the success of the invasion might be greater. However, future studies may shed light on other ecological processes involved in the successful invasion of these arthropods in Chile, mainly linked to the influence of human activity and possible events of facilitation in this country.

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